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Dynamics of Age-Structured Predator–Prey Population Models

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A predator–prey model is investigated in which the prey population is assumed to have age structure and is governed by the McKendrick–von Foerster partial differential equation and the predator population is described by the classical Volterra–Lotka ordinary differential equation. Quite general hypotheses are assumed for the mortality function, the fertility function, and the functional responses of predation. Existence and stability of three biologically meaningful equilibria, corresponding to extinction of both species, persistence of one species prey, and coexistence of two species, are studied. A particular example and some numerical results are given. © 1990 Academic Press, Inc.

1. INTRODUCTION

Predator–prey interactions are ubiquitous in the biological world and are one of the most important topics in ecology. The theoretical study of predation has had a long history beginning with the seminal work of Lotka and Volterra, and continues to be of widespread interest today. Until recently most predator–prey studies have focused on interacting species without age structure (e.g. see May [11], Hsu [8], Freedmann [5], Conway and Smoller [1]). However, as the importance of age structure in populations has become more widely recognized, there is an increasing number of papers dealing with interacting populations with age structure (Gurtin and Levine [6], Cushing and Saleem [4], Pruss [12], Levine [9], Saleem [14], Webb [15]).

The McKendrick–von Foerster partial differential equation is usually used for the study of continuous age structured single-species population models. This is a first-order partial differential equation coupled with a linear integral equation—the so-called renewal equation. Analysis of these

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models is not easy in general. When age structure is introduced into interactions of multispecies, population models can quickly become remarkably complex. Hence, it is understandable that many studies in dynamics of age structured predator–prey populations assumed that age structure was only employed in one species, either in predators (Cushing and Saleem [4]) or in prey (Gurtin and Levine [6], Levine [9], Saleem [14]) and, furthermore, that the mortality function was age-independent or the fertility function took some special forms.

In this paper, we assume that predator population has no age-structure and has dynamics described by the classical Volterra–Lotka ordinary differential equation while the prey population has an age structure which is significant with regard to its growth dynamics and its interaction with the predator. The mortality function, the fertility function, and the interaction functions are assumed to have quite general forms. We study the existence and stability of the trivial and nontrivial equilibrium. Criteria for the extinction of predators and criteria for coexistence are obtained. In the last section, we give a simple example to illustrate our results.

2. Model Formulation

Let $\rho(t, a)$ denote the distribution function of prey so that $\int_\alpha^\beta \rho(t, a)\, da$ is the number of prey with age from α to β and $P(t) = \int_0^\infty \rho(t, a)\, da$ is the total population size of prey. Denote the total number of predators by Q. Assume that the predator population is governed by the classical Volterra–Lotka equation

$$\frac{dQ}{dt} = -bQ + g(P)\, Q,$$

where b is the natural death rate in the absence of prey and $g(P)$ is the conversion rate function of prey deaths into predator births which is assumed to be differentiable and satisfies

$$g(0) = 0, \qquad g'(P) > 0, \qquad \forall P \geqslant 0, \qquad \lim_{P \to \infty} g(P) = k_1 \leqslant \infty. \tag{1}$$

The prey population is assumed to be described by the McKendrick–von Foerster equation

$$\rho_t + \rho_a + D(a, P, Q)\, \rho = 0, \qquad 0 < a \leqslant \infty,$$

$$\rho(t, 0) = \int_0^\infty n(a, P, Q)\, \rho(t, a)\, da,$$

where D is the mortality function and n is the fertility function.

We assume that

$$D = \mu(a) + f_1(P) + f_2(Q), \tag{2}$$

$$n = \beta(a)\, h(Q), \tag{3}$$

where μ is the age-dependent death rate whit $\mu(a) \geqslant 0$, $\forall a > 0$; f_1 is the density-dependent death rate with $f_1(0) = 0$, $f_1'(P) > 0$, $\forall P \geqslant 0$, and $\lim_{P \to \infty} f_1(P) = k_1 \leqslant \infty$; f_2 is the functional response of predators to prey with $f_2(0) = 0$, $f_2'(Q) > 0$, $\forall Q \geqslant 0$, and $\lim_{Q \to \infty} f_2(Q) = k_2 \leqslant \infty$; β is the age-dependent birth rate with $\beta(a) \geqslant 0$, $\forall a > 0$; and h measures the effects of predation on the fertility of prey with $h(0) = 1$, $h'(Q) \leqslant 0$, $\forall Q \geqslant 0$, and $\lim_{Q \to \infty} h(Q) = k_3 \geqslant 0$.

Summarizing these assumptions, we arrive at the following equations:

$$\rho_t + \rho_a = -(\mu(a) + f_1(P) + f_2(Q))\, \rho, \tag{4}$$

$$\rho(t, 0) = h(Q) \int_0^\infty \beta(a)\, \rho(t, a)\, da, \tag{5}$$

$$\frac{dQ}{dt} = -bQ + g(P)\, Q. \tag{6}$$

Using the comparison technique developed in Li [10], we can verify that the solutions ρ and Q of (4–6) satisfy

$$0 \leqslant \rho(t, a) \leqslant \rho^*(t, a),$$

$$0 \leqslant Q(t) \leqslant Q^*(t),$$

where $\rho^*(t, a)$ and $Q^*(t)$ are solutions of

$$\rho_t^* + \rho_a^* = -(\mu(a) + f_1(P^*) + f_2(Q^*))\, \rho^*, \tag{7}$$

$$\rho^*(t, 0) = \int_0^\infty \beta(a)\, \rho^*(t, a)\, da, \tag{8}$$

$$\frac{dQ^*}{dt} = -bQ^* + g(P^*)\, Q^*, \tag{9}$$

with $P^*(t) = \int_0^\infty \rho^*(t, a)\, da$.

From Eqs. (7)–(9), we can derive the following equations for t sufficiently large:

$$\frac{dP^*(t)}{dt} = P^*(t)(r - f_1(P^*) - f_2(Q^*)), \tag{10}$$

$$\frac{dQ^*(t)}{dt} = Q^*(t)(-b + g(P^*)), \tag{11}$$

where r is the real solution of the equation

$$\int_0^\infty \beta(a)\, e^{-\int_0^a \mu(\tau)\, d\tau}\, e^{-ra}\, da = 1. \tag{12}$$

If $r < 0$, the trivial solution $P^* = 0$ and $Q^* = 0$ is stable and, hence, two species go to extinction. This is trivial in mathematics. Therefore, we subsequently, throughout this paper, assume that

$$\int_0^\infty \beta(a)\, e^{-\int_0^a \mu(\tau)\, d\tau}\, da > 1, \tag{H1}$$

which guarantees $r > 0$.

Remark. If $\beta(a) = \beta_0\, ae^{-\alpha a}$, $\mu(a) \equiv \mu$, then the solution of (12) is

$$r = \sqrt{\beta} - \alpha - \mu,$$

corresponding to the result in Gurtin and Levine [6]. In their model, $f_1(P) = 0$, $f_2(Q) = \lambda Q$, $h(Q) = 1$, and $g(P) = cP$:

$$\rho_t + \rho_a = -(\mu + \lambda Q)\, \rho,$$

$$\rho(t, 0) = \int_0^\infty \beta_0 ae^{-\alpha a} \rho(t, a)\, da,$$

$$\frac{dQ}{dt} = -bQ + cPQ,$$

which, obviously, is a special case of the model in this paper. They arrived at a pair of ordinary differential equations

$$\frac{dP}{dt} = \omega P - \lambda PQ,$$

$$\frac{dQ}{dt} = -bQ + cPQ,$$

where $\omega = \sqrt{\beta} - \alpha - \mu$.

2. The Equilibrium $(\rho_0(a), 0)$

To study the case where only the prey population persists, we investigate the behavior of the equilibrium $(\rho_0(a), 0)$ of (4)–(6).

Obviously, the existence of such an equilibrium is equivalent to the existence of the equilibrium of the equations

$$\begin{aligned} &\rho_t + \rho_a = -(\mu(a) + f_1(P))\,\rho, \\ &\rho(t, 0) = \int_0^\infty \beta(a)\,\rho(t, a)\,da. \end{aligned} \tag{13}$$

The solution of (13) has the form of

$$\rho(t, a) = Ce^{r(t-a) - \int_0^a (\tau)\,d\tau - \int_0^t f_1(P(\tau))\,d\tau}$$

for t sufficiently large, where r is the solution of (12). By integrating with respect to a from 0 to ∞, we obtain

$$P(t) = Ce^{rt - \int_0^t f_1(P(\tau))\,d\tau} \int_0^\infty e^{-ra} e^{-\int_0^a \mu(\tau)\,d\tau}\,da.$$

Differentiating $P(t)$, we have

$$\dot{P}(t) = (r - f_1(P))\,P.$$

Hence, there exists an equilibrium $P_0 = f_1^{-1}(r)$ if $k_1 > r$. This is equivalent to

$$\int_0^\infty \beta(a)\,e^{-\int_0^a \mu(\tau)\,d\tau} e^{-k_1 a}\,da < 1.$$

In fact, if we define

$$R(s) = \int_0^\infty \beta(a)\,e^{-\int_0^a \mu(\tau)\,d\tau} e^{-sa}\,da,$$

$R(s)$ is a decreasing function. $R(r) = 1$ and $R(k_1) < 1$ imply $r < k_1$.

Thus, we can state an existence result of the equilibrium $(\rho_0(a), 0)$ as follows.

Theorem 1. *Assume that the hypotheses* (H1) *and*

$$\int_0^\infty \beta(a)\,e^{-\int_0^a \mu(\tau)\,d\tau} e^{-k_1 a}\,da < 1 \tag{H2}$$

hold. Then the system (4)–(6) *has the equilibrium* $(\rho_0(a), 0)$ *where* $P_0 \equiv \int_0^\infty \rho_0(a)\, da$ *satisfies*

$$\int_0^\infty \beta(a)\, e^{-\int_0^a \mu(\tau)\, d\tau} e^{-f_1(P_0)\, a}\, da = 1. \tag{14}$$

Next, we study the stability of $(\rho_0(a), 0)$.

Let $u(t, a) = \rho(t, a) - \rho_0(a)$. Then

$$N(t) \equiv \int_0^\infty u(t, a)\, da = \int_0^\infty \rho(t, a)\, da - \int_0^\infty \rho_0(a)\, da = P(t) - P_0$$

and

$$\begin{aligned} u_t + u_a &= \rho_t + \rho_a - \rho_0'(a) \\ &= -(\mu(a) + f_1(P) + f_2(Q))(u + \rho_0) + \mu(a)\, \rho_0 + f_1(P_0)\, \rho_0 \\ &= -\mu(a)\, u - (f_1(P) + f_2(Q))\, u - \rho_0(f_1(P) - f_1(P_0) + f_2(Q)), \end{aligned} \tag{15}$$

where $\rho_0'(a)$ denotes $d\rho_0(a)/da$.

Expansion of $f_1(P)$ and $f_2(Q)$ at P_0 and 0 yield respectively

$$f_1(P) = f_1(P_0 + N) = f_1(P_0) + f_1'(P_0)\, N + o(N), \tag{16}$$

$$f_2(Q) = f_2'(0)\, Q + o(Q). \tag{17}$$

Write $f_1(P_0) = f_{10}$, $f_1'(P_0) = f_{10}'$, and $f_2'(0) = f_{20}'$, and substitute (16) and (17) into (15) to obtain

$$u_t + u_a \approx -(\mu(a) + f_{10})\, u - f_{10}' \rho_0 N - f_{20}' \rho_0 Q.$$

$$\begin{aligned} u(t, 0) &= \rho(t, 0) - \rho_0(0) \\ &= h(Q) \int_0^\infty \beta(a)(u(t, a) + \rho_0(a))\, da - \rho_0(0) \\ &= h(Q) \int_0^\infty \beta(a)\, u(t, a)\, da + (h(Q) - 1)\, \rho_0(0). \end{aligned} \tag{18}$$

Expanding

$$h(Q) = 1 + h'(0)\, Q + o(Q) \equiv 1 + h_0' Q + o(Q)$$

and substituting it into (18), we arrive at

$$u(t, 0) \approx \int_0^\infty \beta(a)\, u(t, a)\, da + h_0' \rho_0(0)\, Q.$$

The linearization is the following:

$$\begin{aligned} u_t + u_a &= -(\mu(a) + f_{10})\, u - \alpha_1(a)\, N - \alpha_2(a)\, Q, \\ u(t, 0) &= \int_0^\infty \beta(a)\, u(t, a)\, da + \xi Q, \\ \frac{dQ}{dt} &= -\bar{b} Q, \end{aligned} \tag{19}$$

where $\alpha_1(a) = f'_{10}\rho_0(a)$, $\alpha_2(a) = f'_{20}\rho_0(a)$, $\xi = h'_0\rho_0(0)$, and $\bar{b} = b - g(P_0)$.

If $g(P_0) > b$, clearly, $(\rho_0(a), 0)$ is unstable and the predator population is persistent. Assume $g(P_0) < b$. Then, $Q(t) \to 0$, as $t \to \infty$. Thus, asymptotically the dynamics of (19) are governed by

$$\begin{aligned} u_t + u_a &= -(\mu(a) + f_{10})\, u - \alpha_1(a)\, N \\ &= -(\mu(a) + f_{10})\, u - \alpha_1(a) \int_0^\infty u(t, a)\, da \\ u(t, 0) &= \int_0^\infty \beta(a)\, u(t, a)\, da. \end{aligned} \tag{20}$$

Using the method developed by Cushing [2, 3], we suppose

$$u(t, a) = \tilde{u}(a)\, e^{\gamma(t-a)},$$

and define $w = \int_0^\infty \tilde{u}(a)\, e^{-\gamma a}\, da$. Then,

$$\begin{aligned} \tilde{u}'(a) &= -(\mu(a) + f_{10})\, \tilde{u} - \alpha_1(a)\, e^{\gamma a} w \\ \tilde{u}(0) &= \int_0^\infty \beta(a)\, e^{-\gamma a} \tilde{u}(a)\, da. \end{aligned}$$

A solution of the first differential equation for $\tilde{u}(a)$ gives

$$\tilde{u}(a) = e^{-\int_0^a \mu(\tau)\, d\tau - f_{10} a} \left(\tilde{u}(0) - w \int_0^a e^{\int_0^\tau \mu(s)\, ds + f_{10}\tau} \alpha_1(\tau)\, e^{\gamma\tau}\, d\tau \right). \tag{21}$$

Substituting the expression (21) into the expression for $\tilde{u}(0)$ above yields

$$\left(1 - \int_0^\infty \beta(a)\, e^{-\gamma a - f_{10} a - \int_0^a \mu(\tau)\, d\tau} \right) \tilde{u}(0)$$

$$+ w \int_0^\infty \beta(a)\, e^{-\gamma a - f_{10} a - \int_0^a \mu(\tau)\, d\tau} \int_0^a \alpha_1(\tau)\, e^{\gamma\tau} e^{f_{10}\tau + \int_0^\tau \mu(s)\, ds}\, d\tau\, da = 0. \tag{22}$$

Substituting (21) into the definition of w yields

$$\left(\int_0^\infty e^{-\gamma a - f_{10} a - \int_0^a \mu(\tau)\,d\tau}\,da\right)\tilde{u}(0) + \left(-1 - \int_0^\infty e^{-\gamma a - f_{10} a - \int_0^a \mu(\tau)\,d\tau} \int_0^a e^{f_{10}\tau + \int_0^\tau \mu(s)\,ds + \gamma\tau}\,\alpha_1(\tau)\,d\tau\,da\right) w = 0. \tag{23}$$

Define $Y(\gamma, a) = e^{-\gamma a - f_{10} a - \int_0^a \mu(\tau)\,d\tau}$. Then

$$\begin{aligned} &\left(1 - \int_0^\infty \beta(a)\, Y(\gamma, a)\,da\right)\tilde{u}(0) \\ &\quad + w \int_0^\infty \beta(a)\, Y(\gamma, a) \int_0^a \alpha_1(\tau)\, Y^{-1}(\gamma, \tau)\,d\tau\,da = 0, \\ &\left(\int_0^\infty Y(\gamma, a)\,da\right)\tilde{u}(0) \\ &\quad + \left(-1 - \int_0^\infty Y(\gamma, a) \int_0^a \alpha_1(\tau)\, Y^{-1}(\gamma, \tau)\,d\tau\,da\right) w = 0. \end{aligned} \tag{24}$$

Equation (20) has a solution of the form of $u(t, a) = \tilde{u}(a)\, e^{\gamma(t-a)}$ if and only if the system of equations (24) is solvable for $\tilde{u}(0) \not\equiv 0$ and γ, w in the complex plane.

Let $I(\gamma, a) = \int_0^a \rho_0(\tau)\, Y^{-1}(\gamma, \tau)\,d\tau$. We obtain the characteristic equation

$$f'_{10}\left(\int_0^\infty Y(\gamma, a)\,da\right)\left(\int_0^\infty \beta(a)\, Y(\gamma, a)\, I(\gamma, a)\,da\right) + \left(1 - \int_0^\infty \beta(a)\, Y(\gamma, a)\,da\right)\left(1 + f'_{10} \int_0^\infty Y(\gamma, a)\, I(\gamma, a)\,da\right) = 0. \tag{25}$$

Since

$$\rho_0(a) = \rho_0(0)\, e^{-\int_0^a \mu(\tau)\,d\tau - f_{10} a},$$

$$\begin{aligned} I(\gamma, a) &= \int_0^a \rho_0(\tau)\, e^{\gamma\tau + f_{10}\tau + \int_0^\tau \mu(s)\,ds}\,d\tau \\ &= \frac{\rho_0(0)}{\gamma}\,(e^{\gamma a} - 1). \end{aligned}$$

Let

$$E(a) = e^{-f_{10} a - \int_0^a \mu(\tau)\,d\tau}.$$

Then $Y(\gamma, a) = E(a)\, e^{-\gamma a}$. By a simple calculation,

$$\int_0^\infty \beta(a)\, Y(\gamma, a)\, I(\gamma, a)\, da = \frac{\rho_0(0)}{\gamma}\left(1 - \int_0^\infty \beta(a)\, E(a)\, e^{-\gamma a}\, da\right);$$

$$\int_0^\infty Y(\gamma, a)\, I(\gamma, a)\, da = \frac{\rho_0(0)}{\gamma}\left(\int_0^\infty E(a)\, da - \int_0^\infty E(a)\, e^{-\gamma a}\, da\right).$$

Substituting into (25), we get

$$\frac{\rho_0(0)}{\gamma} f'_{10} \int_0^\infty E(a)\, e^{-\gamma a}\, da \left(1 - \int_0^\infty \beta(a)\, E(a)\, e^{-\gamma a}\, da\right)$$
$$+ \left(1 - \int_0^\infty \beta(a)\, E(a)\, e^{-\gamma a}\, da\right).$$
$$\left(1 + \frac{\rho_0(0)}{\gamma} f'_{10}\left(\int_0^\infty E(a)\, da - \int_0^\infty E(a)\, e^{-\gamma a}\, da\right)\right) = 0.$$

Hence the characteristic equation becomes

$$\left(1 - \int_0^\infty \beta(a)\, E(a)\, e^{-\gamma a}\, da\right)\left(1 + \frac{f'_{10}}{\gamma}\rho_0(0) \int_0^\infty E(a)\, da\right) = 0.$$

We need $\tilde{u}(a) \not\equiv 0$, namely $w \neq 0$. This necessarily leads, from (24), to

$$1 - \int_0^\infty \beta(a)\, Y(\gamma, a)\, da = 1 - \int_0^\infty \beta(a)\, E(a)\, e^{-\gamma a}\, da \neq 0,$$

since $\int_0^\infty \beta(a)\, Y(\gamma, a) \int_0^a \alpha_1(\tau)\, Y^{-1}(\gamma, \tau)\, d\tau\, da > 0$. Therefore, the characteristic solution is

$$\gamma = -f'_{10}\rho_0 \int_0^\infty E(a)\, da.$$

Since $f'_1(P_0) > 0$, we obtain the following result.

THEOREM 2. *Assume that the hypotheses* (H1) *and* (H2) *hold. Then the equilibrium* $(\rho_0(a), 0)$ *is asymptotically stable if* $g(P_0) < b$. *It is unstable if* $g(P_0) > b$.

3. COEXISTENCE

In the previous section, we studied the dynamic behavior of the trivial solution $(\rho_0(a), 0)$, which is related to the extinction of predators and to

the possible persistence of the prey population. The purpose of this section is to investigate existence and stability of a nontrivial equilibrium, which is related to coexistence of both predators and prey.

Denote the nontrivial equilibrium by $(\rho^*(a), Q^*)$. It must satisfy the equations:

$$\rho_a^* + (\mu(a) + f_1(P^*) + f_2(Q^*))\,\rho^* = 0, \tag{26}$$

$$\rho^*(0) = h(Q^*) \int_0^\infty \beta(a)\,\rho^*(a)\,da, \tag{27}$$

$$g(P^*) - b = 0, \tag{28}$$

where $P^* = \int_0^\infty \rho^*(a)\,da$.

Equation (28) yields $P^* = g^{-1}(b)$.

From (26),

$$\rho^*(a) = \rho^*(0)\, e^{-\int_0^a \mu(\tau)\,d\tau - f_1(P^*)\,a - f_2(Q^*)\,a}.$$

Substituting into (27), we need to solve

$$\left(1 - h(Q^*) \int_0^\infty \beta(a)\, e^{-\int_0^a \mu(\tau)\,d\tau - f_1(P^*)\,a - f_2(Q^*)\,a}\,da\right)\rho^*(0) = 0$$

for Q^*.

Fix $\rho^*(0)$ and P^*. Let

$$H(z) = 1 - h(z) \int_0^\infty \beta(a)\, e^{-\int_0^a \mu(\tau)\,d\tau - f_1(P^*)\,a - f_2(z)\,a}\,da,$$

and assume that

$$k_3 \int_0^\infty \beta(a)\, e^{-\int_0^a \mu(\tau)\,d\tau - f_1(g^{-1}(b))\,a - k_2 a}\,da < 1. \tag{H3}$$

Then

$$\lim_{z \to \infty} H(z) > 0.$$

Clearly,

$$\frac{dH}{dz} = h(z) f_2'(z) \int_0^\infty a\beta(a)\, e^{-\int_0^a \mu(\tau)\,d\tau - f_1(P^*)\,a - f_2(z)\,a}\,da$$

$$- h'(z) \int_0^\infty \beta(a)\, e^{\int_0^a \mu(\tau)\,d\tau - f_1(P^*)\,a - f_2(z)\,a}\,da.$$

By the assumptions on f_2' and h', $dH/dz > 0$. Hence, if

$$H(0) = 1 - \int_0^\infty \beta(a)\, e^{-\int_0^a \mu(\tau)\, d\tau - f_1(P^*)\, a}\, da < 0, \tag{29}$$

there exists a unique positive solution Q^*.

Now, we claim that $H(0) < 0$ follows if $g^{-1}(b) < f_1^{-1}(r)$, where r is the solution of (12).

Indeed, since

$$R(s) = \int_0^\infty \beta(a)\, e^{-\int_0^a \mu(\tau)\, d\tau}\, e^{-\gamma a}\, da$$

is a decreasing function of s, when $P^* = g^{-1}(b) < f_1^{-1}(r)$, that is $f_1(P^*) < r$, $R(f_1(P^*)) > 1$ which implies $H(0) < 0$.

Summarizing the above statements, we have shown the existence of the nontrivial equilibrium.

THEOREM 3. *Assume that the hypothesis* (H3) *holds and* $R(f_1(g^{-1}(b))) > 1$, *i.e.*,

$$\int_0^\infty \beta(a)\, e^{-\int_0^a \mu(\tau)\, d\tau - f_1(g^{-1}(b))\, a} > 1. \tag{H4}$$

Then the system (4)–(6) *has a unique positive equilibrium* $(\rho^*(a), Q^*)$.

Analyzing the stability of the nontrivial equilibrium $(\rho^*(a), Q^*)$ is more complicated. We again consider perturbations $m(t, a) = \rho(t, a) - \rho^*(a)$ and $W(t) = Q(t) - Q^*$. Then

$$M(t) \equiv \int_0^\infty m(t, a)\, da = P(t) - P^*,$$

$$m_t + m_a = \rho_t + \rho_a - \rho^*(a) \approx -(\mu(a) + f_{1*} + f_{2*})\, m - f_{1*}' \rho^*(a)\, M - f_{2*}' \rho^*(a)\, W,$$

$$m(t, 0)\rho(t, 0) - \rho^*(0) \approx h_* \int_0^\infty \beta(a)\, m(t, a)\, da + \frac{h_*'}{h_*} \rho^*(0)\, W,$$

$$\frac{dW}{dt} = \frac{dQ}{dt} \approx g_*' Q^* M,$$

where f_{1*} denoting $f_1(P^*)$, f_{2*} denoting $f_2(P^*)$, f_{1*}' denoting $f_1'(P^*)$, f_{2*}' denoting $f_2'(Q^*)$, h_* denoting $h(Q^*)$, h_*' denoting $h'(Q^*)$, and g_*' denoting $g'(P^*)$.

Now, we study the asymptotic behavior of the solutions $m(t, a)$ and $W(t)$ of the system of equations:

$$\begin{aligned} &m_t + m_a = -(\mu(a) + f_{1*} + f_{2*})\, m - f'_{1*}\rho^*(a)\, M - f'_{2*}\rho^*(a)\, W, \\ &m(t, 0) = h_* \int_0^\infty \beta(a)\, m(t, a)\, da + \frac{h'_*}{h_*}\rho^*(0)\, W, \\ &\frac{dW}{dt} = g'_* Q^* M. \end{aligned} \tag{30}$$

Integrating $m_t(t, a)$ with respect to a from 0 to ∞, we have

$$\begin{aligned} \frac{dM(t)}{dt} &= \int_0^\infty m_t(t, a)\, da \\ &= -\int_0^\infty m_a(t, a)\, da - \int_0^\infty \mu(a)\, m(t, a)\, da \\ &\quad - \left(f_{1*} + f_{2*} + f'_{1*}\int_0^\infty \rho^*(a)\, da\right) M - f'_{2*}\int_0^\infty \rho^*(a)\, da\, W \\ &= m(t, 0) - \int_0^\infty \mu(a)\, m(t, a)\, da \\ &\quad - (f_{1*} + f_{2*} + f'_{1*}P^*)\, M - f'_{2*}P^* W. \end{aligned}$$

From (30), we arrive at the equations

$$\begin{aligned} \frac{dM(t)}{dt} &= \int_0^\infty (h_*\beta(a) - \mu(a))\, m(t, a)\, da \\ &\quad - (f_{1*} + f_{2*} + f'_{1*}P^*)\, M + \left(\frac{h'_*}{h_*}\rho^*(0) - f'_{2*}P^*\right) W, \\ \frac{dW(t)}{dt} &= g'_* Q^* M. \end{aligned} \tag{31}$$

By the mean value theorem,

$$\int_0^\infty (h_*\beta(a) - \mu(a))\, m(t, a)\, da = (h_*\beta(\theta) - \mu(\theta))\, M,$$

where $0 < \theta = \theta(t) < \infty$.

If we define

$$a_1 = f_{1*} + f_{2*} + f'_{1*} P^*,$$

$$a_2 = f'_{2*} P^* - \frac{h'_*}{h_*} \rho^*(0),$$

$$e = g'_* Q^*,$$

$$\eta(t) = h_* \beta(\theta(t)) - \mu(\theta(t)),$$

the system (31) can be written as the following system:

$$\begin{aligned} \dot{M}(t) &= -a_1 M - a_2 W - \eta(t) M, \\ \dot{W}(t) &= eM. \end{aligned} \tag{32}$$

Write

$$\mathbf{A} = \begin{pmatrix} -a_1 & -a_2 \\ e & 0 \end{pmatrix},$$

$$\mathbf{B}(t) = \begin{pmatrix} \eta(t) & 0 \\ 0 & 0 \end{pmatrix},$$

and

$$\mathbf{X}(t) = \begin{pmatrix} M \\ W \end{pmatrix}.$$

The solution of (32) is

$$\mathbf{X}(t) = e^{\mathbf{A}t} \mathbf{X}(0) + \int_0^t e^{\mathbf{A}(t-\tau)} \mathbf{B}(\tau) \mathbf{X}(\tau) \, d\tau.$$

Suppose that the eigenvalues of $\mathbf{A}$ are λ_1 and λ_2 with $\operatorname{Re} \lambda_1 < \operatorname{Re} \lambda_2$. Then

$$\|\mathbf{X}(t)\| \leqslant K e^{\operatorname{Re} \lambda_2 t} \|\mathbf{X}(0)\| + K \int_0^t e^{\operatorname{Re} \lambda_2 (t-\tau)} \|\mathbf{B}(\tau)\| \cdot \|\mathbf{X}(\tau)\| \, d\tau,$$

where K is a positive constant.

By Gronwall inequality, it follows that

$$\|\mathbf{X}(t)\| \leqslant K \|\mathbf{X}(0)\| \, e^{\operatorname{Re} \lambda_2 t + \int_0^t |\eta(\tau)| \, d\tau}.$$

It is clear that if $a_1^2 \geqslant 4a_2 e$,

$$\lambda_1 = \tfrac{1}{2}(-a_1 - \sqrt{a_1^2 - 4a_2 e}) \leqslant \lambda_2 = \tfrac{1}{2}(-a_1 + \sqrt{a_1^2 - 4a_2 e}) < 0;$$

and if $a_1^2 < 4a_2 e$,

$$\operatorname{Re}\lambda_1 = \operatorname{Re}\lambda_2 = -\tfrac{1}{2}a_1 < 0.$$

Let $\Delta = \max_{0<a<\infty} |h_*\beta(a) - \mu(a)|$. Then $|\eta(t)| \leqslant \Delta$, $\forall t \geqslant 0$. Hence, we obtain the following result.

THEOREM 4. *Assume that the hypotheses* (H3) *and* (H4) *hold. Then the nontrivial equilibrium* $(\rho^*(a), Q^*)$ *is asymptotically stable if either* $a_1^2 < 4a_2 e$ *and* $a_1 > 2\Delta$, *or* $a_1^2 \geqslant 4a_2 e$ *and* $(a_1 - \sqrt{a_1^2 - 4a_2 e}) > 2\Delta$.

These conditions are sufficient. The equilibrium might be unstable under some other circumstances, in which cases, Hopf-bifurcation might occur. We intend to pursue this problem in the future.

4. AN EXAMPLE

In this section, we discuss a simple example. Assume $\mu(a) = \mu_0 + (a/(a+1))$ and $\beta(a) = ae^{-ma}$. Then $\Delta = \mu_0 + 1$.

Simple calculation leads to

$$\int_0^\infty \beta(a)\, e^{-\int_0^a \mu(\tau)\,d\tau}\, da = \frac{1}{(m+\mu_0+1)^2} + \frac{2}{(m+\mu_0+1)^3}.$$

Hence, in order to satisfy the hypothesis (H1), we assume $m + \mu_0 \leqslant 0.5$.

Assume $f_1(x) = Kx$. Then the hypothesis (H2) is satisfied. We take the conversion rate function $g(x) = \delta x/(1+x)$; the functional responses $f_2(x) = \sigma x/(1+x)$ and $h(x) = (1+\omega x)/(1+x)$. (See Holling [7] and Rashevsky [13].)

Equation (14), now, has the form of

$$\frac{m + \mu_0 + KP_0 + 3}{(m + \mu_0 + 1 + KP_0)^3} = 1.$$

The equilibrium P_0 is the solution of this equation.

If $\delta P_0/(1+P_0) < b$, i.e. $P_0 < b/(\delta - b)$, then the equilibrium $(\rho_0(a), 0)$ is stable. This implies that the predator population goes to extinction, but that the prey population persists.

In studying coexistence, since

$$f_{1*} = KP^*, \qquad f_{2*} = \frac{\sigma Q^*}{1+Q^*}, \qquad h_* = \frac{1+\omega Q^*}{1+Q^*},$$

$$f'_{1*} = K, \qquad f'_{2*} = \frac{\sigma}{(1+Q^*)^2}, \qquad g'_* = \frac{\delta}{(1+P^*)^2}, \qquad h'_* = \frac{\omega - 1}{(1+Q^*)^2},$$

in order to have (H3) and (H4) hold, m, μ_0, K, b, δ, and ω need to satisfy

$$\frac{\omega}{\left(m+\mu_0+1+\dfrac{Kb}{\delta-b}+\sigma\right)^2}+\frac{2\omega}{\left(m+\mu_0+1+\dfrac{Kb}{\delta-b}+\sigma\right)^3}<1 \tag{33}$$

and

$$\frac{1}{\left(m+\mu_0+1+\dfrac{Kb}{\delta-b}\right)^2}+\frac{2}{\left(m+\mu_0+1+\dfrac{Kb}{\delta-b}\right)^3}>1. \tag{34}$$

When the inequalities (33) and (34) hold, there is a unique equilibrium Q^* which can be solved from the following equation:

$$\left(m+\mu_0+1+\frac{Kb}{\delta-b}+\left(m+\mu_0+1+\frac{Kb}{\delta-b}+\sigma\right)Q^*\right)^3$$
$$=\left(m+\mu_0+3+\frac{Kb}{\delta-b}\right)(1+Q^*)(1+\omega Q^*). \tag{35}$$

Now

$$a_1^2-4a_2e=\left(\frac{2Kb}{\delta-b}\right)^2+\frac{4Kb\sigma Q^*}{(\delta-b)(1+Q^*)}+\frac{\sigma^2Q^{*2}}{(1+Q^*)^2}$$
$$-\frac{4b\sigma(\delta-b)\,Q^*}{\delta(1+Q^*)^2}-\frac{4(\delta-b)^2\,(1-\omega)\,Q^*}{\delta(1+\omega Q^*)(1+Q^*)}\rho^*(0)$$

and

$$\Delta=\max_{0<a<\infty}\left|h_*ae^{-m a}-\mu_0-\frac{a}{a+1}\right|.$$

Hence, if $a_1^2>4a_2e$ and

$$a_1-\sqrt{a_1^2-4a_2e}>2\Delta,$$

or $a_1^2<4a_2e$ and

$$a_1=\frac{2Kb}{\delta-b}+\frac{\sigma Q^*}{1+Q^*}>2\Delta,$$

the nontrivial equilibrium is stable.

TABLE I

$K=1.5$		$\delta=20$		$\delta=22.5$		$\delta=24.5$	
		P^*	Q^*	P^*	Q^*	P^*	Q^*
$\sigma=0.2$	$\omega=0.5$	0.053	0.160	0.047	0.168	0.043	0.174
$\sigma=0.3$	$\omega=0.7$	0.053	0.147	0.047	0.155	0.043	0.160
$\sigma=0.3$	$\omega=0.15$	0.053	0.152	0.047	0.168	0.043	0.166
$\sigma=0.7$	$\omega=0.15$	0.053	0.112	0.047	0.118	0.043	0.121
$\sigma=0.9$	$\omega=0.15$	0.053	0.098	0.047	0.104	0.043	0.107
$\sigma=0.9$		0.053	0.103	0.047	0.108	0.043	0.112
$K=0.8$		$\delta=20$		$\delta=22.5$		$\delta=24.5$	
		P^*	Q^*	P^*	Q^*	P^*	Q^*
$\sigma=0.3$	$\omega=0.15$	0.053	0.187	0.047	0.192	0.043	0.195
$K=0.4$		$\delta=20$		$\delta=22.5$		$\delta=24.5$	
		P^*	Q^*	P^*	Q^*	P^*	Q^*
$\sigma=0.3$	$\omega=0.15$	0.053	0.207	0.047	0.210	0.043	0.211

By numerical work, some results are obtained as follows. We assume

$$m=0.15, \qquad \mu_0=0.1, \qquad \rho^*(0)=1,$$
$$\sigma=0.3, \qquad b=1.$$

Table I gives stable nontrivial equilibria. From the table, we see that the equilibrium of prey is determined by the conversion rate of prey deaths into predator births and the natural death rate of predators b. An increase of the conversion rate (which means that more prey are to be used to produce predators) gives a larger equilibrium of predators but a smaller equilibrium of prey. However, if the conversion rate is fixed, simply increasing parameters of predation only affects the prey population by decreasing its equilibrium. For example, the bigger σ is or the smaller ω is, the smaller Q^* is. On the other hand, if the carrying capacity of the prey increases (K decreases mathematically), the equilibrium of the predators is increasing as well. These conclusions are similar to those from the classical Lotka–Volterra ordinary differential equation models.

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